

the same for both lineage-specific traits; their Figure 1). Here, the lineage-specific trait can be any character a researcher suspects might affect the propensity for biogeographical dispersal.

The authors recognise that few phylogenetic data sets will be large enough to estimate the large numbers of parameters that matrices of this size define. This poses a challenge to the enterprise of combining biogeographical and lineage-specific traits, and the authors suggest several remedies. A computational approach they do not discuss is reversible-jump Markov chain Monte Carlo (RJ-MCMC). RJ-MCMC [2] can be used in the circumstance the authors describe automatically and correctly to reduce the number of parameters in the Markov transition matrix to the number that the data will support. Users need not constrain parameters *a priori*; RJ-MCMC methods converge on a properly defined Bayesian posterior solution automatically. Box 1 illustrates how RJ-MCMC would work for the case of  $n$  geographical areas and a lineage-specific trait with  $k$  states.

Elsewhere I have described the application of RJ-MCMC to the continuous-time Markov transition model Discrete [3,4], and we have used it in the setting of linguistic evolution to analyse an approximately  $60 \times 60$  matrix of transition probabilities [5]. It is available in the BayesTraits software package ([www.evolution.reading.ac.uk](http://www.evolution.reading.ac.uk)). Matzke [6] also uses RJ-MCMC in a biogeographical context.

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#### References

1. Sukumaran, J. and Knowles, L.L. (2018) Trait-dependent biogeography: (re)integrating biology into probabilistic historical biogeographical models. *Trends Ecol. Evol.* 33, 390–398
2. Green, P.J. (1995) Reversible jump Markov Chain Monte Carlo computation and Bayesian model determination. *Biometrika* 82, 711–732
3. Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. B* 255, 37–45
4. Pagel, M. and Meade, A. (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* 167, 808–825
5. Hruschka, D. et al. (2015) Detecting regular sound changes in linguistics as events of concerted evolution. *Curr. Biol.* 25, 1–9
6. Matzke, N.J. (2014) Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* 63, 951–970

## Forum

### The Dark Side of Animal Phenology

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**Research exploring the timing of recurring biological events has shown that anthropogenic climate change dramatically alters the phenology of many plants and animals. However, we still lack studies on how climate change might alter the phenology of soil invertebrates as well as how this can subsequently affect ecosystem functions.**

#### Climate Change, Phenological Shifts, and Ecosystem Consequences

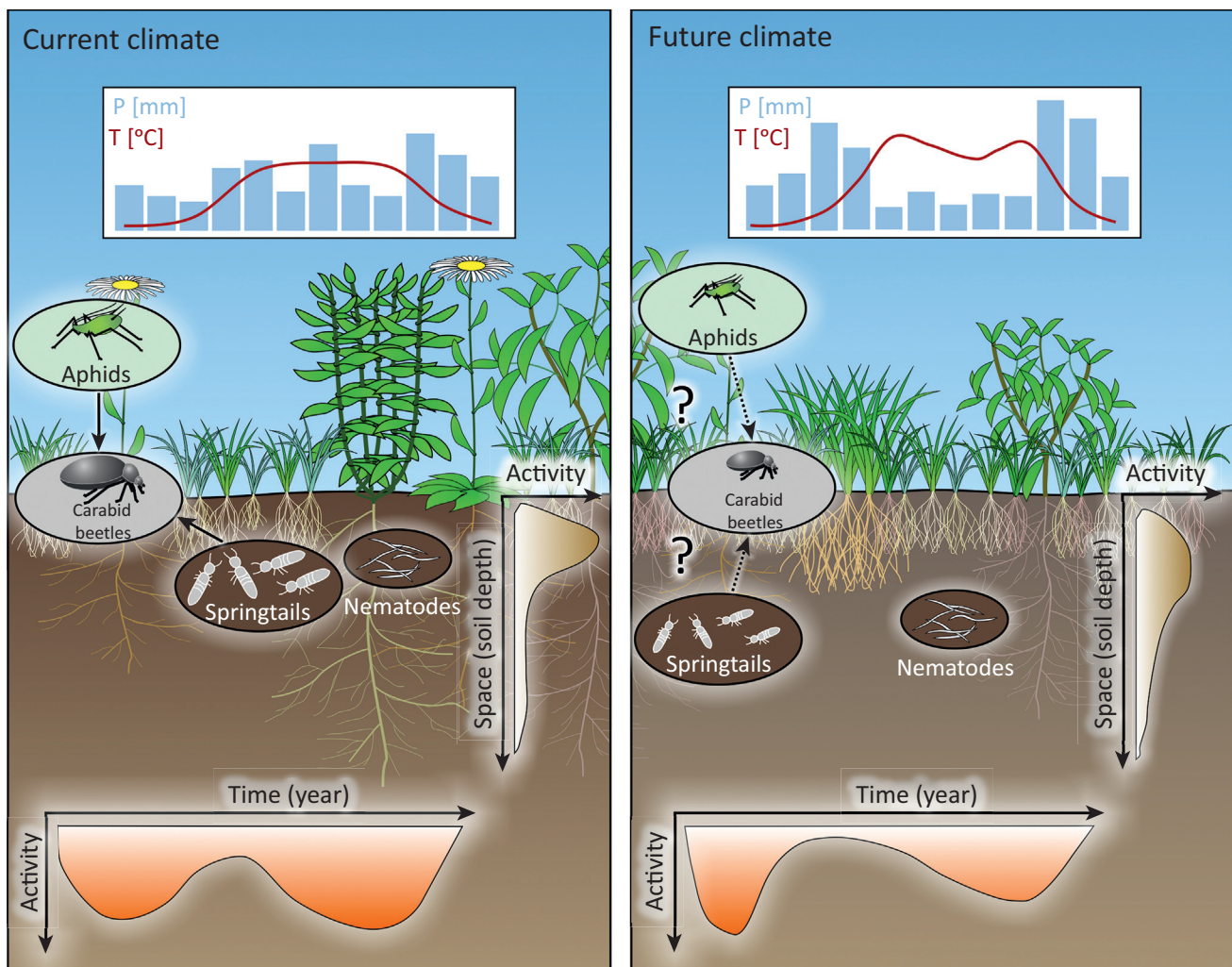
The timing of key life history events in organisms, such as migration, germination, growth, reproduction, senescence, and hibernation, is rapidly changing in response to anthropogenic climate change [1]. Important criteria for such phenological shifts to occur in organisms relate to how tightly their life history events are linked to cues from the abiotic environment [1], diversity and composition of

the local community [2], and how global changes alter the temporal dynamics of both factors. For instance, plant growth often peaks in spring, but the onset of activity by particular species can be advanced or delayed by changes in local environmental conditions [2]. Strong phenological shifts of key organisms are bound to alter the biotic interactions that drive ecosystem functions like resource uptake and production of biomass. For example, reduced temporal synchrony between consumer and resource species, when a resource species tracks the seasonal shifts and consumers do not, can lead to demographic changes, species extinctions, and altered ecosystem productivity [3]. Two recent global syntheses on phenological shifts in plants (reviewed in [4]) and animals (meta-analysis in [5]) confirmed that climate variables, namely temperature and precipitation, which determine the seasonality in a given region, are central to driving phenological shifts in species. Presumably due to their inaccessibility, soil invertebrate animals (soil animals hereafter) have rarely been incorporated into phenological research [5] despite of their sensitivity to both temperature and precipitation [6], and their crucial roles in driving multiple ecosystem functions [6–8]. Here, we highlight the importance of studying the phenology of soil animals for improving our understanding of global change impacts on ecosystem functioning in terrestrial environments.

#### The ‘Black Box’ of Soil Animal Phenology

Soil ecologists have studied the temporal dynamics of soil organisms for decades, mostly focusing on seasonal population dynamics, temporal predictability of soil community composition, the drivers of temporal variability in soil communities, as well as the resistance and resilience of soil communities and functions in response to environmental disturbances [7–10]. However, the temporal dynamics

have rarely been related to phenology of soil animals and their potential response to environmental drivers (but see work on highly synchronized species with pulsed emergence; e.g., periodical cicadas), and the available information has not been synthesized so far. Notably, in some cases, soil phenology is just a matter of turning soil activity off and on (i.e., soil microbial activity responds rapidly to root enzymes and soil moisture). So, plants are particularly crucial drivers of activity patterns of soil organisms as they create hotspots (space) and hot moments (time) of resource availability [11]. Yet, larger-bodied soil animals often alter their vertical distribution along the soil profile in response to variations in temperature



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**Figure 1. Conceptual Figure of the Relationships among Seasonality, Community Composition, and Soil Animal Phenology as Affected by Climate Change.** Timing and strength of soil animal interactions as well as identity of their interaction partners depend on time of year and environmental conditions (abiotic and biotic). Global changes in environmental conditions, such as alterations in temperature ( $T$  [°C]) and precipitation ( $P$  [mm]) patterns shown in the top panels, influence the phenology of aboveground–belowground interactions with direct and indirect (i.e., via plant–soil feedback) implications for ecosystem functioning. Climate change can alter temporal and spatial activity patterns of soil animals, such as decreased activity during warmer and drier summer months and reduced activities in drier topsoils, respectively. These shifts can alter the links between aboveground and belowground food webs, as indicated by unknown future feeding links of carabid beetles to aphids (aboveground) and springtails (belowground). Belowground herbivory (represented by nematodes) and its consequences might change due to alterations in spatial and temporal feeding interactions (nematode icon moves in space and time in the figure). Moreover, shifts in plant and animal community structure (indicated by a dominance of graminoids in the future climate) as well as shifts in body sizes of soil animals (indicated by the reduced body size in the future climate) in response to climate change is likely to have consequences for soil animal phenology. Taken together, these climate-induced abiotic and biotic alterations exemplify a few of the many potential drivers of soil animal phenology.

and precipitation, which changes both the spatial and the temporal aspects of their interaction partners (Figure 1). For instance, soil animals often move to deeper soil layers during adverse environmental conditions, such as drought, and thus can influence plant species with deeper roots during drier time periods. Examining potential ecosystem consequences of changes in soil animal phenology then depends not only on geographic variation in climate change drivers, such as precipitation, temperature, and freeze–thaw cycles, but also on changes in depth of interactions across the soil profile [12], as well as with aboveground interaction partners like predators (Figure 1).

Available inferences on soil animal phenology have thus far mostly been based on repeated soil community samplings (which is destructive to monitoring of experimental plots, because they involve soil core samplings) [7,8], or assessments of community-level decomposition

activity [6], and only rarely by monitoring populations of soil animals using nondestructive sampling methods [13]. This fuels the challenge to identify shifts in phenology as well as matches and mismatches of activity patterns among soil animals. Thermal sensitivity of metabolism and activity are related to body size, and soil animals span a great range of size distribution (from microfauna-like protists to macrofauna-like earthworms), which might cause trophic mismatches of animals with different phenological shifts. Exploring these potential mismatches would require data documenting the timing of population-level events, while integrative means to measure, for instance, decomposition activity would rather reflect community-level responses.

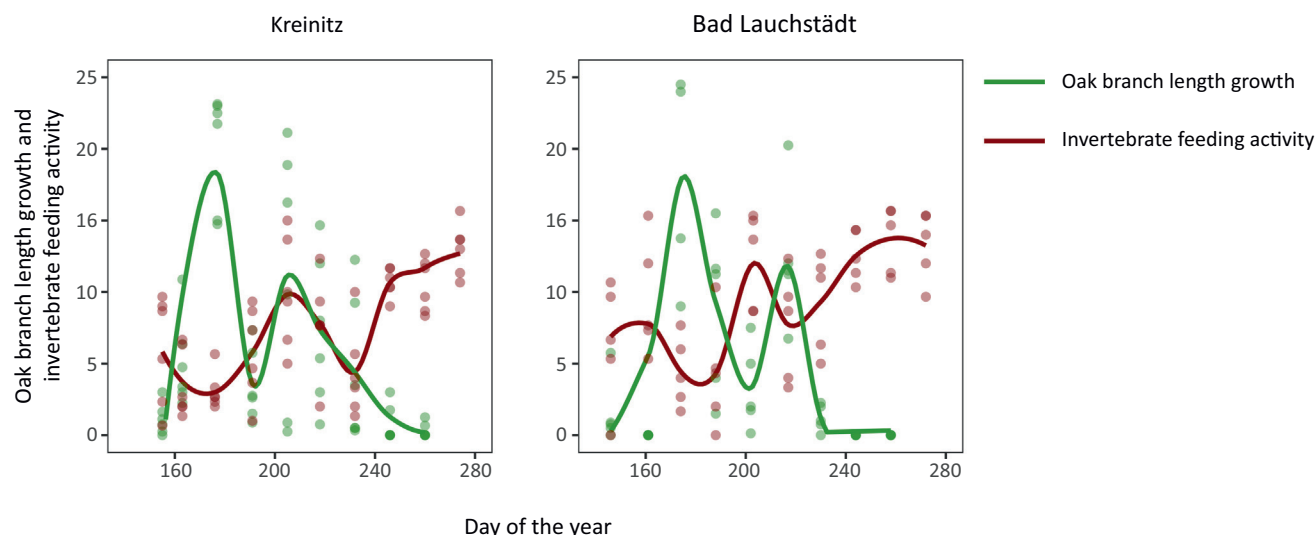
### The Phenology of Above- and Belowground Interactions: An Oak Case Study

To exemplify these potential plant and soil animal phenology linkages, we present results of a phytometer experiment using

clonal oaks that have clear temporal oscillations of resource inputs to the soil [14], in which we studied shoot growth phenology and soil invertebrate feeding activity (i.e., decomposition of a cellulose-based substrate; [6]) at two locations in Germany (Kreinitz and Bad Lauchstädt). Our results show that plant growth phenology and invertebrate activity across the growing season can be linked, that is, they show anticyclical patterns (Bad Lauchstädt), but they also can be disconnected (Kreinitz) (Figure 2). These results indicate pronounced phenological patterns in soil invertebrate feeding activity with a heretofore unknown interplay between direct climate and indirect plant effects.

### Ways Forward: Merging New Concepts and Methods

A recent meta-analysis indicates that soil animals and the functions they drive might be particularly prone to phenological shifts under climate change, as temperature effects were reported to be most



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**Figure 2. Matches and Mismatches of Plant and Soil Animal Phenology.** Growth phenology of clonal oaks [14] via oak branch length growth assessments [cm] of 5-year-old trees ( $n = 5$  per site) as well as soil invertebrate feeding activity using bait lamina strips (number of empty bait holes ranges between 0 and 16; [6]) were assessed every 2 weeks from April to October in 2014 at two locations in Germany (Kreinitz and Bad Lauchstädt). These oaks show alternating endogenous rhythmic growth patterns of root and shoot flushes [14]. Low levels of oak branch length growth indicate periods of root growth [14], which might thus denote pulses of carbon inputs to and biological activity in the soil [11]. If oak root flushes determined soil invertebrate feeding activity, this would be indicated by anticyclical patterns of the two phenology measures (such as the case in Bad Lauchstädt).

pronounced in invertebrates and small-bodied animals above the ground [3]. Moreover, areas experiencing the most severe climate changes and that are prone to freezing and thawing of soils will be particularly sensitive to changes in soil animal activity. However, the extant knowledge gap in phenological shifts of soil animals currently limits our capacity to predict ecosystem responses to climate change. Much previous work on above-ground animal phenology has focused on monitoring of populations or simple pairs of species interactions (i.e., plant–herbivore, plant–pollinator, and host–parasite). Notably, studying such species-specific interactions in soils is elusive, and new approaches will likely focus on community phenology [6]. One exception might be the recent methodological advances in automated, nondestructive sensing techniques like the EDAPHOLOG system [13]—allowing the online measurement of belowground microarthropods and their body size—will facilitate the study of soil animal phenology. This method allows repeated sampling of soil animal communities without disturbing the soil. In the future, it might be conceivable to arrange this belowground pitfall trap in a way to monitor soil animal communities in different soil depths, and to quantify soil animal phenology responses to climate change in space and time (Figure 1). Other novel techniques, such as nondestructive spectroscopic analyses of soil communities and activities (e.g., visible and near-infrared reflectance spectroscopy and mid-infrared spectroscopy) need to be refined and applied to field conditions. The establishment of several globally distributed, experimental networks on the ecosystem-level consequences of global environmental change (such as Drought-Net<sup>†</sup>) will help identify global patterns in how above- and belowground phenologies might relate to each other. Recent synthesis works [4,5] provide a predictive framework for soil animal phenological responses according to their

traits like trophic position [3] and body size [5], in order to explore if the general patterns that apply to aboveground animals are also relevant for those in the soil, which will help illuminate the ‘dark side of animal phenology’.

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### Resources

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### References

- Forrest, J. and Miller-Rushing, A.J. (2010) Toward a synthetic understanding of the role of phenology in ecology and evolution. *Phil. Trans. Roy. Soc. B* 365, 3101–3112
- Wolf, A.A. *et al.* (2017) Flowering phenology shifts in response to biodiversity loss. *Proc. Natl. Acad. Sci.* 114, 3463–3468
- Thackeray, S.J. *et al.* (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535, 241
- Volkovich, E.M. *et al.* (2014) Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. *New Phytol.* 201, 1156–1162
- Cohen, J.M. *et al.* (2018) A global synthesis of animal phenological responses to climate change. *Nat. Clim. Change* 8, 224–228
- Thakur, M.P. *et al.* (2018) Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nat. Clim. Change* 8, 75–78

- Bengtsson, J. (1994) Temporal predictability in forest soil communities. *J. Anim. Ecol.* 63, 653–665
- Wardle, D.A. (1998) Controls of temporal variability of the soil microbial biomass: a global-scale synthesis. *Soil Biol. Biochem.* 30, 1627–1637
- Takeda, H. (1987) Dynamics and maintenance of collembolan community structure in a forest soil system. *Res. Popul. Ecol.* 29, 291–346
- Dunger, W. *et al.* (2004) Development of soil fauna at mine sites during 46 years after afforestation. *Pedobiologia* 45, 243–271
- Kuzakov, Y. and Blagodatskaya, E. (2015) Microbial hotspots and hot moments in soil: concept & review. *Soil Biol. Biochem.* 83, 184–199
- Pries, C.E.H. *et al.* (2017) The whole-soil carbon flux in response to warming. *Science* 355, 1420–1423
- Dombos, M. *et al.* (2017) EDAPHOLOG monitoring system: automatic, real-time detection of soil microarthropods. *Methods Ecol. Evol.* 8, 313–321
- Herrmann, S. *et al.* (2015) Endogenous rhythmic growth in oak trees is regulated by internal clocks rather than resource availability. *J. Exp. Bot.* 66, 7113–7127

## Forum

### Sensory Exploitation, Sexual Dimorphism, and Human Voice Pitch

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**Selection for low male voice pitch is generally assumed to occur because it is a valid cue of formidability. Here we summarize recent empirical challenges to this hypothesis. We also outline an alternative account in which selection for low male voice pitch is a byproduct of sensory exploitation.**

The most popular hypothesis for why men have lower voice pitch (Box 1) than women is that low male voice pitch has been selected for because it is a valid cue of critical aspects of formidability, such as physical strength and large body size, meaning that men with lower voice pitch will be more successful in intrasexual